EVOLUTION

Flocks of African fishes

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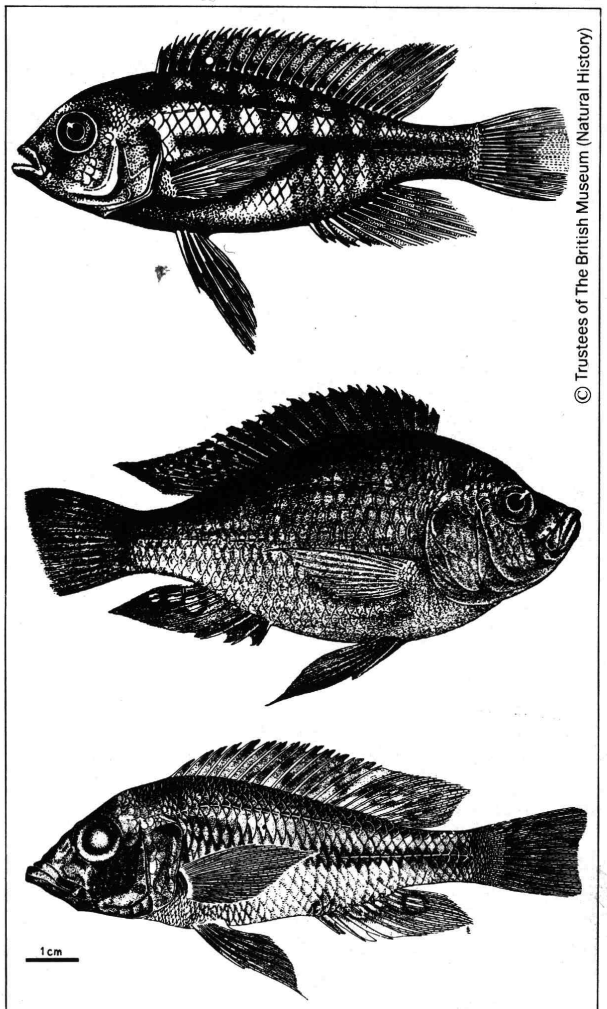
MORPHOLOGICAL and molecular evolution can march to the beats of different drummers. Thus horseshoe crabs, 'living fossils' that have changed little in morphology over tens of millions of years, exhibit 'normal' patterns of genetic variation and divergence in proteins and DNA[1,2], whereas humans and chimps, which differ so obviously in anatomy and way of life, are more than 99 per cent identical in polypeptide sequences[3]. Even against such examples, the apparent decoupling of morphological and molecular evolution reported for African rift-valley lake fishes on page 550 of this issue is stunning. Meyer *et al.*[4] report that 14 assayed species, representing nine genera of cichlids endemic to Lake Victoria, show almost no differentiation at some 800 nucleotide positions in the cytochrome *b* gene, two transfer RNA genes and the normally highly variable portion of the control region of mitochondrial (mt) DNA. The mean level of mtDNA sequence divergence among these species and genera is less than that within a single species of horseshoe crab[2], or within the human species, which itself exhibits low intraspecific mtDNA differentiation compared to many vertebrates, including other fishes.

The cichlid species flocks in Lake Victoria and other African rift lakes have long intrigued biologists as prime examples of 'explosive evolution'[5]. Lake Victoria is less than one million years old, yet it contains some 200 species of cichlids, almost all of which are endemic. This assemblage exhibits moderate diversity in external morphology (see figure), but far more striking are the ecological and trophic specializations represented[6,7]. There are algae grazers, plankton and detritus feeders, pharyngeal snail crushers, and insect and fish predators. Some species are paedophages, eating fish embryos by engulfing the snout of a mouth-brooding female and forcing her to jettison the brood. One species feeds on scales rasped from tail fins, while another (in Lake Malawi) plucks the eyes from other fishes. The discovery of a near lack of mtDNA differentiation among representative Lake Victoria cichlids implies that this remarkable kind of organismal diversity evolved very recently (within the past 200,000 years), probably from a single common ancestor within the lake.

The hypothesis of recent monophyly for the Lake Victoria flock is further supported by mtDNA comparisons involving other African cichlids[4]. For example, assayed species in nearby Lake Malawi differed from those in Lake Victoria by more than 50 base substitutions, whereas the Lake Victoria cichlids differed from one another by an average of only three mtDNA mutations. Among 20 members surveyed of the 200 or so endemic cichlids in Lake Malawi, two distinct mtDNA lineages were observed, but these remained much more closely related to one another than to any non-Malawi cichlids examined. Thus the molecular findings appear to eliminate an alternative picture for the Lake Victoria and Lake Malawi species flocks — that they might represent the polyphyletic products of numerous invasions by taxa that had become highly differentiated before each lake's formation.



Examples of cichlid species from Lake Victoria assayed by Meyer *et al.*[4]. Top, *Ptyochromis sauvagei*; middle, *Lipochromis obesus*; bottom, *Astatotilapia piceatus*. (Reproduced from ref. 7.)

The phylogeny and taxonomy of the African cichlid flocks have long been under dispute. Traditionally, most of the described species (over 500 of them) were placed in a single genus, *Haplochromis*, but in recent years a morphological reanalysis based on hennigian principles prompted a taxonomic splitting into a large number of genera and subgenera[7]. Many of these taxa have representatives in at least four of the African great lakes, such that "the overall picture is one of a super-flock comprised of several lineages whose members cut across the boundaries imposed by the present-day lake shores"[8]. The molecular findings of Meyer *et al.*[4] stand in stark opposition to this concept. If the mtDNA results are corroborated and extended to many additional haplochromine species, yet another taxonomic realignment will be in order, one in which the lineages recognized would coincide almost perfectly with the present-day lake-shore boundaries.

The phylogenetic findings with mtDNA set the stage for further research on the ecology and genetics of African great-lake fishes. Did the intra-lacustrine speciations take place sympatrically, or did they occur at times of geomorphological subdivision of a lake basin? Is there a simple genetic basis to the ecological and morphological shifts, and are particular morpho-genes involved? Could at least some of the morphological shifts represent phenotypic or ontogenetic plasticity within species, as has been suggested for trophic polymorphisms in some New World cichlid fishes[9]? (Additional assays of nuclear genes are needed to decide whether the gene pools of all morpho-species are truly distinct.) Is there some peculiarity in the genetic makeup, behaviour or ecology of cichlid fishes that predisposes them to explosive evolutionary radiation, whereas other fish taxa in these lakes appear to evolve at normal rates? What are the ecological and behavioural ramifications of habitat partitioning by so many closely related forms? These are all obvious but difficult questions. The findings of Meyer *et al.*[4] at least show that there really is a phen-

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omenal pattern of within-lake evolutionary radiation to be understood.

The cichlids of the great African lakes are the most spectacular of a small number of fish species flocks in drainage basins scattered around the world[10]. Most are threatened with extinction from anthropogenic causes, and indeed the cyprinid flock in the Philippines' Lake Lanao has already been lost. The African cichlids are also in rapid decline, primarily because of the introduction of exotic predatory fish. The great African rift lakes and their faunas will someday disappear as tectonic plate movements continue to split the continent. Premature closure of this extraordinary evolutionary theatre and play through human activities would be a biological tragedy of the first order. □

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